

Three new species of *Agaricus* (Agaricaceae, Agaricales) from southern China

Shi-en Wang¹, Si-ang Chen², Hai-chen Huang³, Dong-mei Lin¹, Peng-hu Liu¹

¹ National Engineering Research Center of Juncao Technology, College of JunCao Science and Ecology, Fujian Agriculture and Forestry University, Fuzhou, China

² College of Agriculture, Fujian Agriculture and Forestry University, Fuzhou, China

³ College of Life Sciences, Fujian Agriculture and Forestry University, Fuzhou, China

Corresponding author: Peng-hu Liu (phliu1982@163.com)

Abstract

The genus *Agaricus* is the most species-rich genus within the Agaricaceae, comprising more than 500 species globally. Here, we describe three new species of *Agaricus* based on morphological and multi-locus (ITS + nrLSU + *tef1-a*) phylogenetic analyses: *Agaricus aurantifibrillosus*, *A. fafuinus* and *A. shenzhenensis*. *Agaricus aurantifibrillosus* and *A. fafuinus* were collected at Fujian province, while *A. shenzhenensis* was discovered in Shenzhen City, Guangdong Province. The morphological descriptions of each new species are accompanied by basidiomata photographs, and illustrations of microscopic structures.

Key words: *Agaricus*, morphology, multi-locus phylogeny, new species, taxonomy

Introduction

Agaricus L. is the type genus of the family Agaricaceae Chevall. (Donk 1962; Parra 2008; Kerrigan 2016; Zhao et al. 2016; Bau 2018). Species within *Agaricus* are primarily saprophytic fungi, typically inhabiting forest ecosystems or grasslands (Zhao et al. 2011; Chen et al. 2017). However, recent studies have expanded their known ecological niches, with documentation of lignicolous taxa such as *A. subiculosus* Miller, Angelini, L.A. Parra & Linda J. Chen growing on decaying wood substrates (Parra et al. 2024a). Although a minority of *Agaricus* species are toxic and may provoke gastrointestinal distress, the majority exhibit significant edible and medicinal value (Wu et al. 2019; Boxshall et al. 2021; Jaichaliaw et al. 2021; He et al. 2022). Currently, several species within *Agaricus* are utilized for food and nutraceutical applications, including *A. bisporus* (J.E. Lange) Imbach, *A. flocculosipes* R.L. Zhao, Desjardin, Guinb. & K.D. Hyde and *A. subrufescens* Peck (Wisitrassameewong et al. 2012; Zhao et al. 2012, 2016).

As outlined in our previous studies (Wang 2024; Wang and Bau 2024), the taxonomy of *Agaricus* has experienced substantial development over the past two decades, due to the incorporation of molecular characters and phylogenetic methodologies to the traditional morphological characters. To date, *Agaricus* comprises six subgenera, 27 sections (Zhao et al. 2016; Chen et al. 2017;



Academic editor: Kentaro Hosaka

Received: 29 March 2025

Accepted: 27 May 2025

Published: 25 June 2025

Citation: Wang S-e, Chen S-a, Huang H-c, Lin D-m, Liu P-h (2025) Three new species of *Agaricus* (Agaricaceae, Agaricales) from southern China. MycoKeys 119: 47–66. <https://doi.org/10.3897/mycokeys.119.154278>

Copyright: © Shi-en Wang et al.

This is an open access article distributed under terms of the Creative Commons Attribution License (Attribution 4.0 International – CC BY 4.0).

Callac and Chen 2018; He et al. 2018a; Parra et al. 2018a; Ortiz-Santana et al. 2021; Hussain et al. 2022). This study focuses on three subgenera and three sections within *Agaricus*, viz., *A. sect. Agaricus* in *A. subg. Agaricus*, *A. sect. Catenulati* in *A. subg. Pseudochitonina*, and *A. sect. Minores* in *A. subg. Minores*.

The type species of *A. sect. Agaricus* is *A. campestris* L., which shows the following taxonomic characteristics: pileus surface unchanging or slightly yellowing, rarely rufescent on touching; context often turning pink or strongly reddening; odor usually indistinct or mushroomy, sometimes anise; annulus superous or intermediate, simple or double, membranous or fibrillose; KOH and Schäffer's reactions negative on white areas of the surface of the pileus; cheilocystidia absent or indistinct, basidia-like, some species abundant, large, globose, piriform or ovoid, never catenulate (Zhao et al. 2016).

The type species of *A. sect. Catenulati* is *A. arabiensis* S. Hussain & Al-Sadi. Species of the section are characterized by: medium-sized basidiomata; white context unchanging when bruised or handled; a phenolic odor; a slightly yellow KOH reaction and negative Schäffer's reactions; cheilocystidia globose to subglobose or broadly ellipsoid, the anteterminal elements subglobose or cylindrical, forming a chain-shaped structure (Hussain et al. 2022).

Agaricus sect. Minores with the type species *A. comtulus* Fr.. This section has the following phenotypic characters: basidiomes often slender, small-to-medium sized; surface of pileus often discoloring yellow on touching; context often turning yellow on exposure; odor of anise or bitter almonds; annulus superous, simple, thin, fragile; KOH and Schäffer's reactions positive; cheilocystidia simple, clavate, pyriform, sometimes absent, scattered or rare (Zhao et al. 2016).

The genus *Agaricus* has attracted increasing attention from taxonomists in recent years. In 2024, 26 novel species were described globally (Arya and Pradeep 2024; Crous et al. 2024; Bashir et al. 2024; Guzmán-Guillermo et al. 2024; Liang et al. 2024; Liu et al. 2024; Nawaz et al. 2024; Palestina-Villa et al. 2024; Parra et al. 2024a, 2024b; Ullah et al. 2024) following our previous publication on 11 January (Wang and Bau 2024). Notably, *A. baiyunensis*, *A. cainus* and *A. praeclarefibrillosus* were discovered in southern China (Liang et al. 2024). Additionally, *A. totalaiensis* M. Ishaq, M. Fiaz & A.N. Khalid is currently under review (<https://preprints.arphahub.com/article/133080/>, accessed on 4 March 2025).

In this study, we further expand the known diversity of *Agaricus* in China by describing three new species based on morphological characteristics and molecular phylogenetic analyses, i.e., *A. aurantifibrillosus*, *A. fafuinus* and *A. shenzhenensis*.

Materials and methods

Morphological studies

The macro-morphological characteristics of the species were described using notes and photographs taken from fresh basidiomata collected during field collecting. The color description of the fresh basidiomata follows the Methuen Handbook of Color (Kornerup and Wanscher 1978). Microstructures

were observed using a Nikon differential interference contrast (DIC) optical microscope (Nikon Corporation, Japan). Basidiospore descriptions followed the methodologies outlined in previous studies (Wang and Bau 2024). The symbol “(a) b–c (d)” is used to describe the size of basidiospores, where the “b–c” range represents 90% of the measured values, while the “a” and “d” are extreme values. “[Xav = e × f]” indicates the average size of basidiospores. “Q” refers to the ratio of length to width of a single basidiospore from the side view, and “Qav” refers to the average value of “Q” of all specimens. The morphological descriptions of taxa followed the methods outlined in previous studies (Parra 2013; Kerrigan 2016; Zhao et al. 2016). The voucher specimens of this study are deposited in the fungarium of the Fujian Academy of Agricultural Sciences (FFAAS), China.

Phylogenetic studies

Genomic DNA was extracted from specimens using the DNA extraction kit (Fuzhou Meilisha Biotechnology Co., Ltd., Fuzhou, China). The primer pairs ITS1F/ITS4 (White et al. 1990; Gardes and Bruns 1993), LR0R/LR5 (Moncalvo et al. 2000) and EF1-983F/EF1-1567R (Rehner and Buckley 2005) were used to amplify the sequences of three DNA regions, ITS, nrLSU and *tef1-α*, respectively. The polymerase chain reaction (PCR) procedure was based on the protocol described by Mou and Bau (2021).

The newly generated sequences were deposited in the National Center of Biotechnology Information (NCBI) database (<https://www.ncbi.nlm.nih.gov/>). Sequences of phylogenetically related taxa within the same section were retrieved from NCBI and incorporated into phylogenetic analyses (Table 1). Finally, species falling within the clades of the species described in this study were selected and integrated to construct new multi-locus phylogenetic trees. *Heinemannomyces* sp. ZRL185 was used as an outgroup (Zhao et al. 2016; Ortiz-Santana et al. 2021). The ITS, nrLSU, and *tef1-α* sequences were independently aligned using the Q-INS-i algorithm via the MAFFT v.7.205 (Kato and Standley 2013) online server (<https://mafft.cbrc.jp/alignment/server/>). Sequence alignments were manually adjusted in BioEdit v7.1.3.0 (Hall 1999) and subsequently concatenated for the ITS, nrLSU, and *tef1-α* regions using PhyloSuite v1.2.2 (Zhang et al. 2020). ModelFinder v2.2.0 (Kalyaanamoorthy et al. 2017) was used to select the best-fit model using BIC criterion.

Maximum likelihood (ML) phylogenies were inferred using IQ-TREE for 5000 ultrafast bootstraps, as well as the Shimodaira–Hasegawa–like approximate likelihood-ratio test (Guindon et al. 2010; Nguyen et al. 2015). Bayesian Inference (BI) phylogenies were inferred using MrBayes 3.2.6 (Ronquist et al. 2012) under partition model, in which the initial 25% of sampled data were discarded as burn-in. Analyses were run until convergence criteria were met (average standard deviation of split frequencies <0.01). The phylogenetic tree was visualized using FigTree v1.4.3 (<http://tree.bio.ed.ac.uk/software/figtree/>) and edited using Adobe Illustrator 2021 (Adobe, San Jose, CA, USA). Bootstrap support (BS) values ≥ 50% and Bayesian posterior probability (PP) values ≥ 0.70 are indicated on branches (BS/PP).

Table 1. Sequences used in the phylogenetic analysis. Bold refers to the sequences produced from this study. “T” refers to the type specimen. “—” means no relevant genetic information.

| Taxon | Voucher specimen | Country | GenBank accession numbers | | | References |
|---|---------------------|--------------|---------------------------|-----------------|-----------------|--------------------------|
| | | | ITS | nrLSU | <i>tef1-a</i> | |
| <i>Agaricus andrewii</i> | RWK 2096 | The USA | KJ877740 | — | — | (Kerrigan 2016) |
| <i>A. andrewii</i> | RWK 1997 T | The USA | KJ877738 | — | — | (Kerrigan 2016) |
| <i>A. andrewii</i> | FFAAS 3387 | China | PV247928 | PV242028 | PV261082 | In this study |
| <i>A. andrewii</i> | FFAAS 3388 | China | PV247929 | — | PV261083 | In this study |
| <i>A. andrewii</i> | FFAAS 3389 | China | PV247930 | — | — | In this study |
| <i>A. arabiensis</i> | SQUH-DRB001 | Oman | OM971854 | — | — | (Hussain et al. 2022) |
| <i>A. arabiensis</i> | SQUH-SNT007 T | Oman | OM971855 | OM971859 | ON568585 | (Hussain et al. 2022) |
| <i>A. argenteus</i> | ZRL20181598 | China | MN604437 | — | — | (Liu et al. 2020) |
| <i>A. argenteus</i> | QL20170054 | China | MN604422 | — | — | (Liu et al. 2020) |
| <i>A. argenteus</i> subsp. <i>annetteae</i> | RWK 2025 | The USA | KJ877746 | — | — | (Kerrigan 2016) |
| <i>A. argenteus</i> subsp. <i>argenteus</i> | RWK 1998 | The USA | KJ877744 | — | — | (Kerrigan 2016) |
| <i>A. argyropotamicus</i> | RWK 2017 | The USA | KJ877748 | — | — | (Kerrigan 2016) |
| <i>A. argyropotamicus</i> | F2047 | France | JF727849 | — | — | (Zhao et al. 2011) |
| <i>A. aristocratus</i> | ZRL20162182 | China | MN604412 | — | — | (Liu et al. 2020) |
| <i>A. aristocratus</i> | ZRL20162183 | China | MN604413 | — | — | (Liu et al. 2020) |
| <i>A. aurantifibrillosus</i> | FFAAS 3390 T | China | PV247931 | PV242029 | PV261078 | In this study |
| <i>A. aurantifibrillosus</i> | FFAAS 3391 | China | PV247932 | PV242030 | PV261079 | In this study |
| <i>A. aurantifibrillosus</i> | FFAAS 3392 | China | PV247933 | PV242031 | PV261080 | In this study |
| <i>A. badiosquamulosus</i> | LAH35751 T | Pakistan | ON137221 | OP831149 | OP903342 | (Bashir et al. 2024) |
| <i>A. badiosquamulosus</i> | LAH35752 | Pakistan | ON137222 | OP831150 | OP903343 | (Bashir et al. 2024) |
| <i>A. baiyunensis</i> | GDGM 87953 T | China | ON075801 | ON140627 | ON122987 | (Liang et al. 2024) |
| <i>A. braendlei</i> | MO479453 | The USA | OP470057 | — | — | — |
| <i>A. campestris</i> | LAPAG370 T | Spain | KM657927 | KR006607 | KR006636 | (Zhou et al. 2016) |
| <i>A. carassaii</i> | AH56324 T | Italy | NR_182917 | — | — | (Bashir et al. 2024) |
| <i>A. cf. altipes</i> | RWK 1976 | The USA | KJ877750 | — | — | (Kerrigan 2016) |
| <i>A. cf. altipes</i> | RWK 1977 | The USA | KJ877751 | — | — | (Kerrigan 2016) |
| <i>A. colpeteii</i> | TL2424 T | Australia | JX984565 | — | — | (Bashir et al. 2024) |
| <i>A. cupreobrunneus</i> | CA 87 | France | DQ182532 | — | — | (Liu et al. 2020) |
| <i>A. cupreobrunneus</i> | LAPAG322 | Spain | JQ824136 | — | — | (Liu et al. 2020) |
| <i>A. dunensis</i> | LAH35747 T | Pakistan | ON137217 | OP835847 | OP903344 | (Bashir et al. 2024) |
| <i>A. dunensis</i> | LAH36807 | Pakistan | ON158596 | OP835848 | OP903345 | (Bashir et al. 2024) |
| <i>A. fafuinus</i> | FFAAS 3393 T | China | PV247934 | PV242032 | PV261084 | In this study |
| <i>A. fafuinus</i> | FFAAS 3394 | China | PV247935 | PV242033 | PV261085 | In this study |
| <i>A. gastronevadensis</i> | SFSU DM Reno T | The USA | NR144997 | — | — | (Liu et al. 2020) |
| <i>A. griseicephalus</i> | SFSU F-021060 T | The USA | NR144998 | — | — | (Liu et al. 2020) |
| <i>A. griseicephalus</i> | ZRL20150352 | China | MN604416 | — | — | (Liu et al. 2020) |
| <i>A. iesu-et-marthae</i> | LAPAG41 | Spain | KF447904 | — | — | (Bashir et al. 2024) |
| <i>A. incultorum</i> | RWK 2109 | The USA | KJ877766 | — | — | (Kerrigan 2016) |
| <i>A. indicus</i> | TBGT16128 T | India | OR661746 | — | — | (Arya and Pradeep 2024) |
| <i>A. indicus</i> | TBGT15735 | India | OR661749 | — | — | (Arya and Pradeep 2024) |
| <i>A. lannaensis</i> | SDBR-NK0564 T | Thailand | MW255657 | MW255674 | MW264834 | (Jaichaliaw et al. 2021) |
| <i>A. lannaensis</i> | SDBR-NK0584 | Thailand | MW255738 | MW262926 | MW264835 | (Jaichaliaw et al. 2021) |
| <i>A. malakandensis</i> | ViL-60 T | Pakistan | OQ845443 | OQ845442 | OR296711 | (Nawaz et al. 2024) |

| Taxon | Voucher specimen | Country | GenBank accession numbers | | | References |
|---|---------------------|--------------|---------------------------|-----------------|-----------------|--------------------------|
| | | | ITS | nrLSU | <i>tef1-a</i> | |
| <i>A. malakandensis</i> | ViL-68 | Pakistan | OQ845480 | OQ845500 | — | (Nawaz et al. 2024) |
| <i>A. malakandensis</i> | LD2012162 | Thailand | KT951337 | KT951493 | KT951563 | (Zhao et al. 2016) |
| <i>A. minipurpureus</i> | ZRL2010058 T | China | KX657043 | KX656953 | KX684947 | (He et al. 2018b) |
| <i>A. minipurpureus</i> | ZRL2013342 | China | KX657008 | KX656944 | KX684977 | (He et al. 2018b) |
| <i>A. moellerianus</i> | GQ 1 | The USA | KJ877767 | — | — | (Kerrigan 2016) |
| <i>A. palodensis</i> | TBGT17483 T | India | OR661748 | — | — | (Arya and Pradeep 2024) |
| <i>A. palodensis</i> | TBGT18550 | India | OR661747 | — | — | (Arya and Pradeep 2024) |
| <i>A. parviumbrus</i> | MEL:2382858 T | Australia | KP012732 | — | — | (Bashir et al. 2024) |
| <i>A. porphyrocephalus</i> subsp. <i>alpinus</i> | AH47618 T | Italy | MK511988 | — | — | (Parra et al. 2018b) |
| <i>A. porphyrocephalus</i> subsp. <i>alpinus</i> | LAPAG1030 | Italy | MK511989 | — | — | (Parra et al. 2018b) |
| <i>A. porphyrocephalus</i> subsp. <i>pallidus</i> | SFSU F-020927 T | The USA | NR145000 | — | — | (Liu et al. 2020) |
| <i>A. porphyrocephalus</i> subsp. <i>pallidus</i> | RWK 2211 | The USA | KJ877771 | — | — | (Liu et al. 2020) |
| <i>A. porphyrocephalus</i> subsp. <i>porphyrocephalus</i> | JM 1 | The USA | KJ877768 | — | — | (Liu et al. 2020) |
| <i>A. porphyrocephalus</i> subsp. <i>porphyrocephalus</i> | RWK 2088 | The USA | KJ877769 | — | — | (Liu et al. 2020) |
| <i>A. shenzhenensis</i> | FFAAS 3397 T | China | PV247938 | PV242035 | PV261076 | In this study |
| <i>A. shenzhenensis</i> | FFAAS 3398 | China | PV247939 | PV242036 | PV261077 | In this study |
| <i>A. thailandensis</i> | SDBR-CJ0118 T | Thailand | MW255675 | MW255677 | MW264832 | (Jaichaliaw et al. 2021) |
| <i>A. violaceopunctatus</i> | LAH35767 T | Pakistan | ON158593 | OP835850 | — | (Bashir et al. 2024) |
| <i>A. violaceopunctatus</i> | LAH21719 | Pakistan | ON158595 | — | OP903347 | (Bashir et al. 2024) |
| <i>A. wayanadensis</i> | TBGT18860 T | India | OR661750 | — | — | (Arya and Pradeep 2024) |
| <i>A. wayanadensis</i> | TBGT18790 | India | OR661751 | — | — | (Arya and Pradeep 2024) |
| <i>A. zhangyensis</i> | QL20170111 T | China | MN604426 | — | — | (Liu et al. 2020) |
| <i>A. zhangyensis</i> | QL201701152 | China | MN604427 | — | — | (Liu et al. 2020) |
| <i>Agaricus</i> sp. | FFAAS 3399 | China | PV247940 | PV242037 | PV261081 | In this study |
| <i>Agaricus</i> sp. | ZRL20162141 | China | MN604414 | — | — | (Liu et al. 2020) |
| <i>Agaricus</i> sp. | RWK 1923 | The USA | KJ877772 | — | — | (Liu et al. 2020) |
| <i>Heinemannomyces</i> sp. | ZRL185 | Thailand | KT951346 | KT951527 | KT951657 | (Zhao et al. 2016) |

Results

Phylogenetic analyses

In this study, 30 sequences were generated including 11 ITS sequences, 9 nrLSU sequences, and 10 *tef1-a* sequences. The multi-locus dataset (ITS + nrLSU+ *tef1-a*) of *Agaricus* had an aligned length of 2157 bp (ITS subset: 1–725 bp; nrLSU subset: 726–1595 bp; *tef1-a* subset: 1596–2157 bp) total characters including gaps. Alignment has 70 sequences with 2157 columns, 637 distinct patterns 407 parsimony-informative, 155 singleton sites, 1595 constant sites. The alignment was submitted to Figshare (<https://figshare.com/s/778e265dd87f6d6f83b0>).

In this study, Bayesian inference (BI) and maximum likelihood (ML) phylogenetic trees were reconstructed using a concatenated dataset comprising ITS, nrLSU, and *tef1-a* sequences. BI and ML analysis resulted in a very similar topology, so the ML tree is provided in this study (Fig. 1). For the construction of the maximum likelihood (ML) phylogenetic tree, the best-fit substitution model (TIM2+F+I+G4, without partitioning) was selected using BIC criterion.

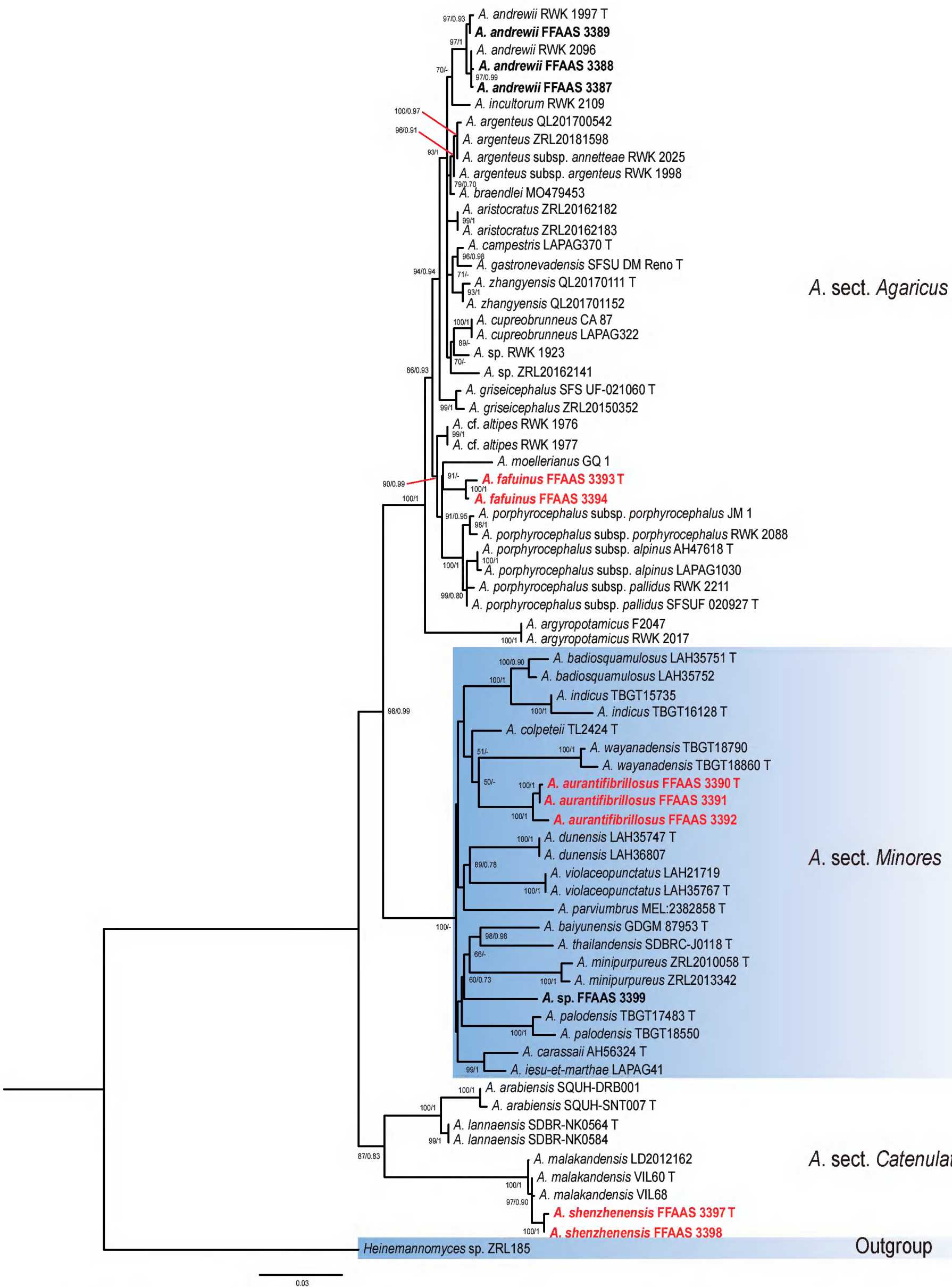


Figure 1. Multi-locus phylogenetic tree of *Agaricus* obtained from the maximum likelihood analysis (ML) based on ITS, nrLSU, and *tef1-α* sequence data. “T” refers to the type specimen. Bold refers to the sequences produced from this study. Red font refers to the new species.

Similarly, for the Bayesian inference (BI) phylogeny, a partitioned model (edge-linked) was optimized using BIC, with the following partitions: HKY+F+G4 for ITS, GTR+F+I+G4 for nrLSU, and K2P+G4 for *tef1-α*.

The phylogenetic tree revealed three major clades, corresponding to three sections: *A. sect. Agaricus*, *A. sect. Catenulati* and *A. sect. Minores*. *A. fafuinus* and *A. moellerianus* Bon formed a sister clade (BS/PP = 91/-) in *A. sect. Agaricus*. Within *A. sect. Catenulati*, *A. shenzhenensis* and *A. malakandensis* formed a sister clade with a strong support value (BS/PP = 97/0.90). Within *A. sect. Minores*, *A. aurantifibrillosus* is phylogenetically close to *A. colpeteii* T. Lebel and *A. wayanadensis*. Despite low support values, *A. aurantifibrillosus* forms a distinct clade.

Taxonomy

***Agaricus aurantifibrillosus* P.H. Liu & S.E. Wang, sp. nov.**

MycoBank No: 858060

Figs 2A, B, 3

Etymology. *aurantifibrillosus* (Latin), referring to the pileus covered with arranged orange (5A8) or brownish yellow (5C8) fibrillose squamules.

Holotypus. CHINA • Fujian Province, Fuzhou City, Fuzhou National Forest Park, 2 October 2024, 26°10'41"N, 119°16'19"E, alt. 280 m, Shi-En Wang, E2410232 (FFAAS 3390).

Diagnosis. This species is characterized by its pileus covered with orange (5A8) or brownish yellow (5C8) scattered fibrillose squamules, elongate basidiospores ($Q_{av} = 1.70$), and abundant cheilocystidia.

Description. Pileus 3.6–6.2 cm in diameter, 0.2–0.3 cm thick at the center, truncate conical to plane, surface dry, white (5A1) or orange white (5A2), covered with scattered arranged orange (5A8), brownish yellow (5C8) fibrillose squamules, denser at disc, showing brownish orange (6C8) or brown (6E8), margin appendiculate by annulus remnants. Context of the pileus white (6A1), with no special odor. Lamellae 0.2–0.4 cm broad, pastel red (9A4) then reddish brown (8E8) later brownish black (8F8), free, crowded, intercalated with numerous lamellulae. Stipe 5.6–8.6 × 0.4–1.3 cm, hollow, clavate, with white (6A1) rhizomorphs, provided with an annulus in its upper third, above the annulus white (6A1), below the annulus with white (6A1), orange (5A8) floccose squamules, becoming dark yellow (4C8) on touching or bruising. Annulus superior, white (6A1), simple, membranous, easy falling out.

Basidiospores (4.6)4.7–5.7(5.9) × (2.7)2.8–3.3(3.6) μm, [$X_{av} = 5.2 \times 3.1$ μm], $Q = 1.50$ –1.93, $Q_{av} = 1.70$, ellipsoid to elongate-ellipsoid, smooth, thick-walled, brown, guttulate. Basidia 14–18 × 5–7 μm, clavate, 4(2)-spored, sterigmata 2–4 μm long. Cheilocystidia abundant, nearly globose, oblong, sphaeropedunculate, or broadly clavate, 12–34 × 10–20 μm, with pale yellowish intracellular pigment. Pleurocystidia absent. Pileipellis a cutis of cylindrical, slightly constricted at the septa, pale yellowish hyphae, 4–9 μm in diameter.

Habitat and distribution. Gregarious or scattered in broad-leaved and bamboo forests during autumn. Currently, it has only been documented in Fujian Province, China.



Figure 2. The photographs of fresh basidiomata of *Agaricus* species in this study. **A.** *A. aurantifibrillosus* (FFAAS 3390); **B.** *A. aurantifibrillosus* (FFAAS 3391); **C.** *A. fafuinus* (FFAAS 3393); **D.** *A. fafuinus* (FFAAS 3394); **E.** *A. shenzhenensis* (FFAAS 3397); **F.** *A. shenzhenensis* (FFAAS 3398). Scale bars: 1 cm.

Additional specimens measured. CHINA • Fujian Province, Fuzhou City, Fujian Agriculture and Forestry University, 5 October 2024, Shi-En Wang, E2410524 (FFAAS 3391) and E2410525 (FFAAS 3392).

Notes. *Agaricus aurantifibrillosus* belongs to *A.* (subg. *Minores*) sect. *Minores*. *Agaricus aurantipileatus* T. Bau & S.E. Wang in *A.* sect. *Arvenses* shares morphological similarities with *A. aurantifibrillosus*. However, *A. aurantipileatus* can

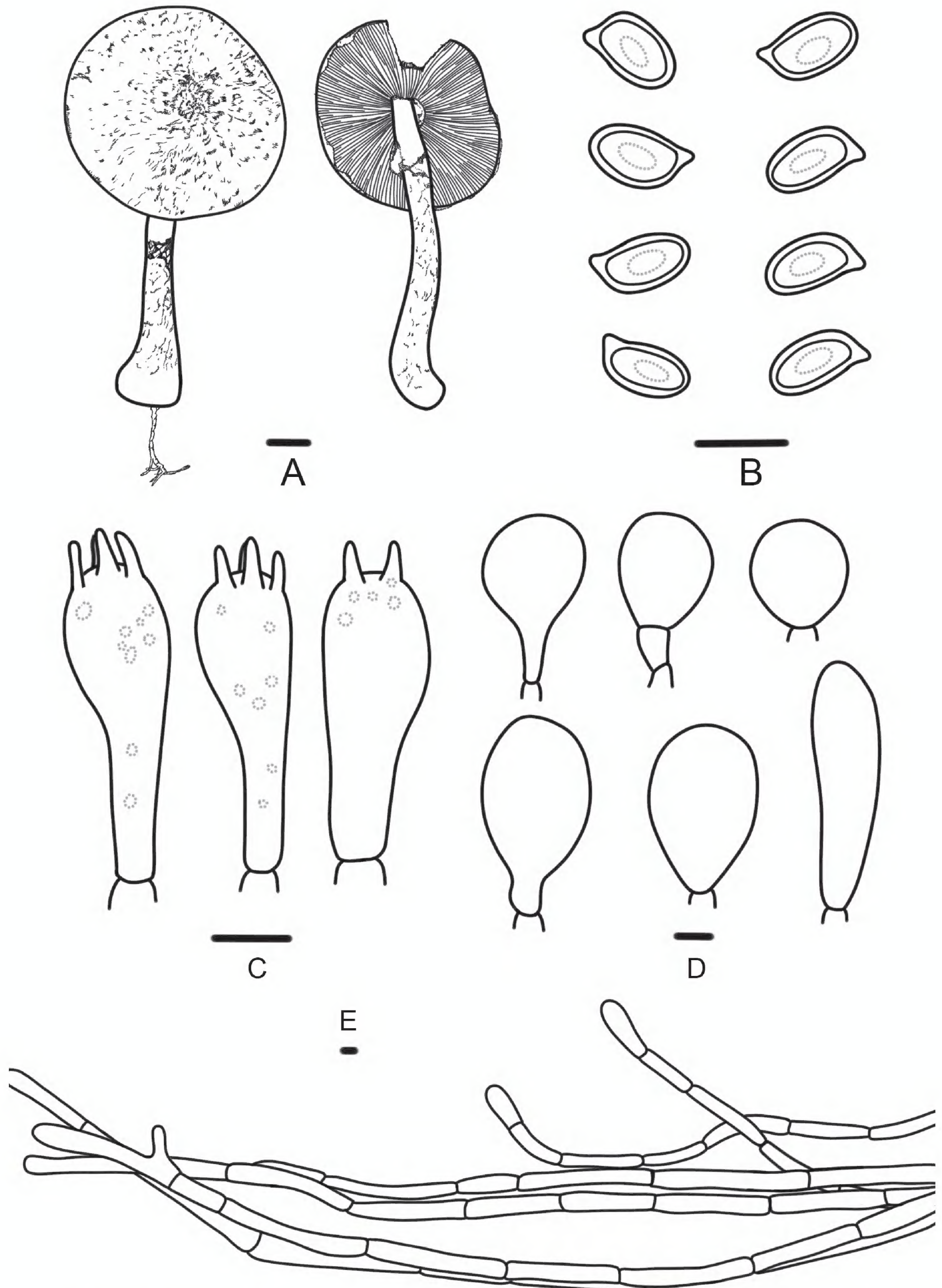


Figure 3. *Agaricus aurantifibrillosus* (FFAAS 3390, FFAAS 3391); **A.** Basidiomata; **B.** Basidiospores; **C.** Basidia; **D.** Cheilocystidia; **E.** Pileipellis. Scale bar: 1 cm (**A**); 5 μ m (**B–E**).

be distinguished by its double annulus, smaller spore Q value ($Q = 1.17\text{--}1.36$), and sometimes catenulate cheilocystidia (Wang and Bau 2024).

In the multi-locus phylogenetic tree (Fig. 1), *A. aurantifibrillosus* clusters with *A. colpeteii* T. Lebel and *A. wayanadensis*, albeit with low statistical support, and this may be due to the lack of sequences in the related taxa. *Agaricus colpeteii* is a gasteroid *Agaricus* species with basidia not observed (Lebel 2013). *Agaricus wayanadensis* differs in having a pileus surface covered with brown squamules and a smaller spore Qav value ($Q_{av} = 1.58$) (Arya and Pradeep 2024).

***Agaricus fafuinus* P.H. Liu & S.E. Wang, sp. nov.**

MycoBank No: 858061

Figs 2C, D, 4

Etymology. Derived from the acronym FAFU (Fujian Agriculture and Forestry University), where the type specimens of this species were collected.

Holotypus. CHINA • Fujian Province, Fuzhou City, Fujian Agriculture and Forestry University, 4 March 2024, 26°08'N, 119°24'E, alt. 30 m, Si-Ang Chen, CSA299 (FFAAS 3393).

Diagnosis. This species is characterized by its pileus and stipe covered with brown (7D5) or fox red (8D7) fibrils or fibrillose squamules, elongate basidiospores ($Q_{av} = 1.63$), and abundant cheilocystidia.

Description. Pileus 3.4–5.5 cm in diameter, 0.2–0.4 cm thick at the center, truncate conical to plane, surface dry, white (5A1), brownish gray (7C2), covered with brown (7D5) or fox red (8D7) fibrils or with fibrillose squamules, concentrically arranged, denser and reddish brown (8E8) at disc, margin appendiculate by annulus remnants. Context of the pileus, white (6A1), with no special odor. Lamellae 0.2–0.3 cm broad, first pastel red (9A4), then reddish brown (8E8), later brownish black (8F8), free, crowded, intercalated with numerous lamellulae. Stipe 2.2–4.5 × 0.6–1.5 cm, nearly cylindrical, hollow, with white (6A1) rhizomorphs, provided with an annulus in its upper half, above the annulus white (6A1), below the annulus covered towards the base with concolorous squamules with the pileus surface. Annulus superior, white (6A1) to reddish brown (8E8), simple, membranous, persistent.

Basidiospores (5.7)6.0–7.9(8.2) × (3.5)3.7–5.0(5.1) μm, [$X_{av} = 6.8 \times 4.2$ μm], $Q = 1.46\text{--}2.03$, $Q_{av} = 1.63$, ellipsoid to cylindrical, smooth, thick-walled, brown, guttulate. Basidia 17–25 × 6–9 μm, clavate, 4(2)-spored, sterigmata 1–3 μm long. Cheilocystidia abundant, nearly globose, broadly clavate, or pyriform, 10–23 × 7–13 μm, hyaline. Pleurocystidia absent. Pileipellis a cutis of cylindrical, slightly constricted at septa, light brown hyphae, 6–12 μm wide.

Habitat and distribution. Gregarious in bamboo forests or grass during spring. Currently, it has only been known from Fujian Province, China.

Additional specimens measured. CHINA • Fujian Province, Fuzhou City, Fujian Agriculture and Forestry University, 23 March 2024, Si-Ang Chen, CSA314 (FFAAS 3394).

Notes. *Agaricus fafuinus* belongs to *A.* (subg. *Agaricus*) sect. *Agaricus*. *Agaricus fafuinus* exhibits variable pileus surface: specimen CSA299 possesses fibrils, while CSA314 displays fibrillose squamules. However, molecular data confirm their conspecificity, suggesting that these morphological differences

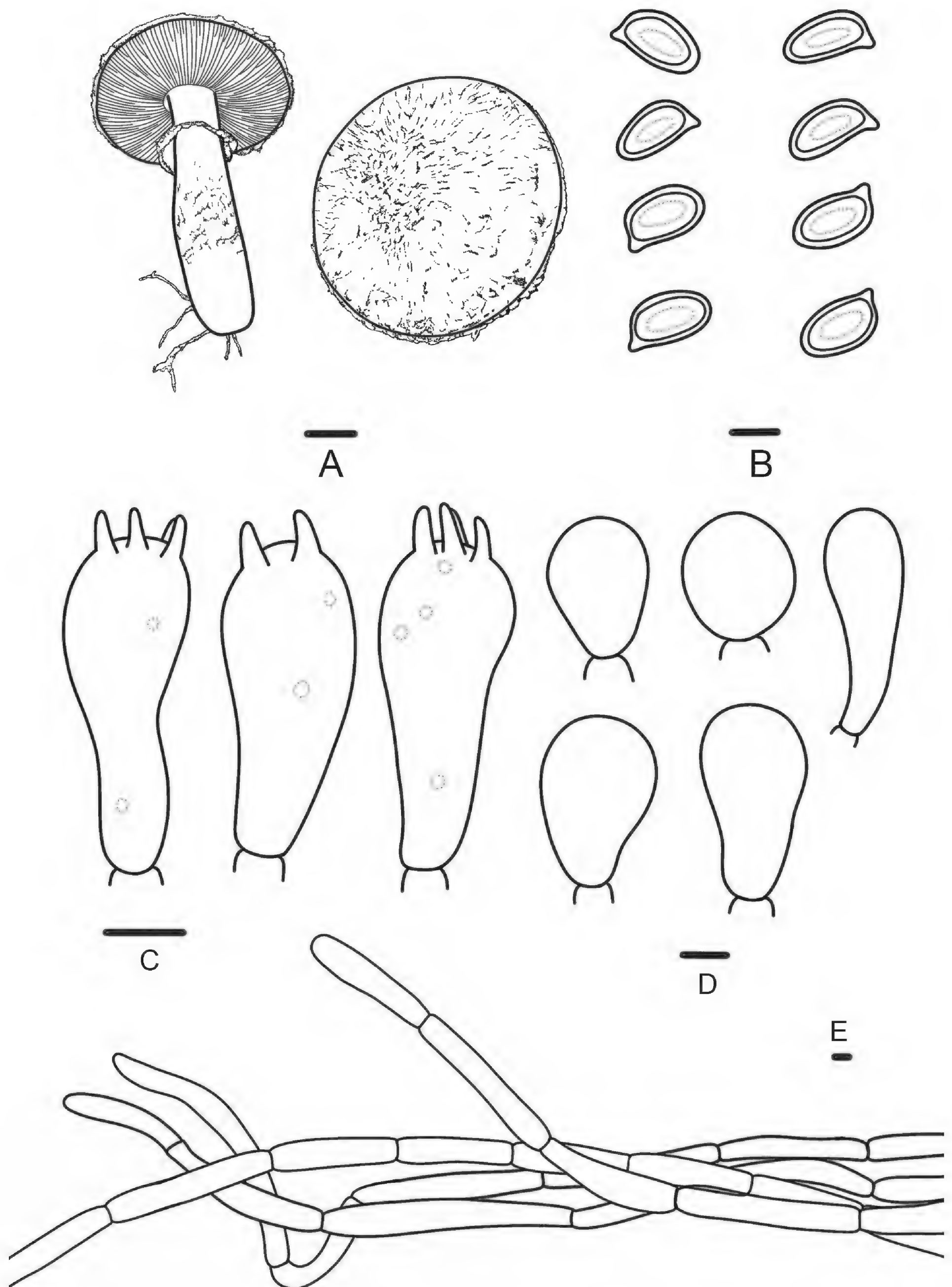


Figure 4. *Agaricus fafuinus* (FFAAS 3393, FFAAS 3394); **A.** Basidiomata; **B.** Basidiospores; **C.** Basidia; **D.** Cheilocystidia; **E.** Pileipellis. Scale bar: 1 cm (**A**); 5 μm (**B–E**).

may result from humidity variations. Specimen CSA299 was collected post-rain-fall and likely it was exposed to precipitation, whereas specimen CSA314 was obtained under dry conditions. Initially, we thought we had mixed up the specimen numbers, but after thorough verification, this turned out to be accurate.

In the multi-locus phylogenetic tree (Fig. 1), *A. fafuinus* and *A. moellerianus* Bon form a sister clade with good support. However, *A. moellerianus* is distinguished by its subglabrous white pileus, smooth stipe, rounder basidiospores ($Q_{av} = 1.22$), and broadly clavate cheilocystidia resembling basidioles (Kerrigan 2016).

***Agaricus shenzhenensis* P.H. Liu & S.E. Wang, sp. nov.**

MycoBank No: 858063

Figs 2E, F, 5

Etymology. *shenzhenensis* (Latin), meaning from shenzhen city where the holotype specimen was collected.

Holotypus. CHINA • Guangdong Province, Shenzhen City, Lianhuashan Park, 29 April 2024, 22°33'23"N, 114°3'13"E, alt. 100 m, Cheng-Cheng, 20240430 (FFAAS 3397).

Diagnosis. Distinguished by the pileus adorned with brownish gray (6E2) fibrillose squamules, context becoming yellow (3B8) on cutting, stipe base tapering and covered with brownish gray (6E2) fibrillose squamules, predominantly 2-spored basidia.

Description. Pileus 2.5–6.5 cm in diameter, 0.5–0.8 cm thick at the center, hemispherical, truncate conical to plane, applanate with a slightly depressed center when mature, surface dry, white (2A1), grayish white (2B1), entirely covered with appressed, concentrically arranged, triangular, brownish gray (6E2) fibrillose squamules, scattered towards the margin in age, denser taupe (4F1), black (2F1) at the disc, margin entire, appendiculate by annulus remnants. Context of the pileus white (6A1), becoming yellow (3B8) on cutting, odor unknown. Lamellae 0.5–0.7 cm broad, first pale red (9A3) then reddish brown (8E8), later brownish black (8F8), free, crowded, intercalated with numerous lamellulae. Stipe 4.5–11.5 × 0.5–2.0 cm, cylindrical, tapering downwards, hollow, with short white (6A1) rhizomorphs, provided with an annulus in its upper part, above the annulus white (6A1), below the annulus the upper half white and the lower half covered with dense adpressed brownish grey (6E2) squamules concolorous with the pileus surface. Annulus superior, white (6A1) to brownish black (8F8), simple, membranous, persistent.

Basidiospores (5.8)6.1–7.3(7.5) × (3.8)4.0–4.3(4.4) μm , [$X_{av} = 6.8 \times 4.2 \mu\text{m}$], $Q = 1.41–1.87$, $Q_{av} = 1.61$, ellipsoid to elongate-ellipsoid, smooth, brown, thick-walled, guttulate. Basidia 25–33 × 8–10 μm , clavate, 2(4)-spored, sterigmata 2–3 μm long. Cheilocystidia abundant, broadly clavate, oblong or pyriform, 22–50 × 10–22 μm . Pleurocystidia absent. Pileipellis a cutis of cylindrical, slightly constricted at the septa, light brown hyphae, 4–7 μm wide.

Habitat and distribution. Gregarious or clustered in grass or broad-leaved forests during spring. Currently, it is only known from Guangdong Province, China.

Additional specimens measured. CHINA • Guangdong Province, Shenzhen City, Lianhuashan Park, 29 April 2024, Cheng-Cheng, 20240430-1 (FFAAS 3398).

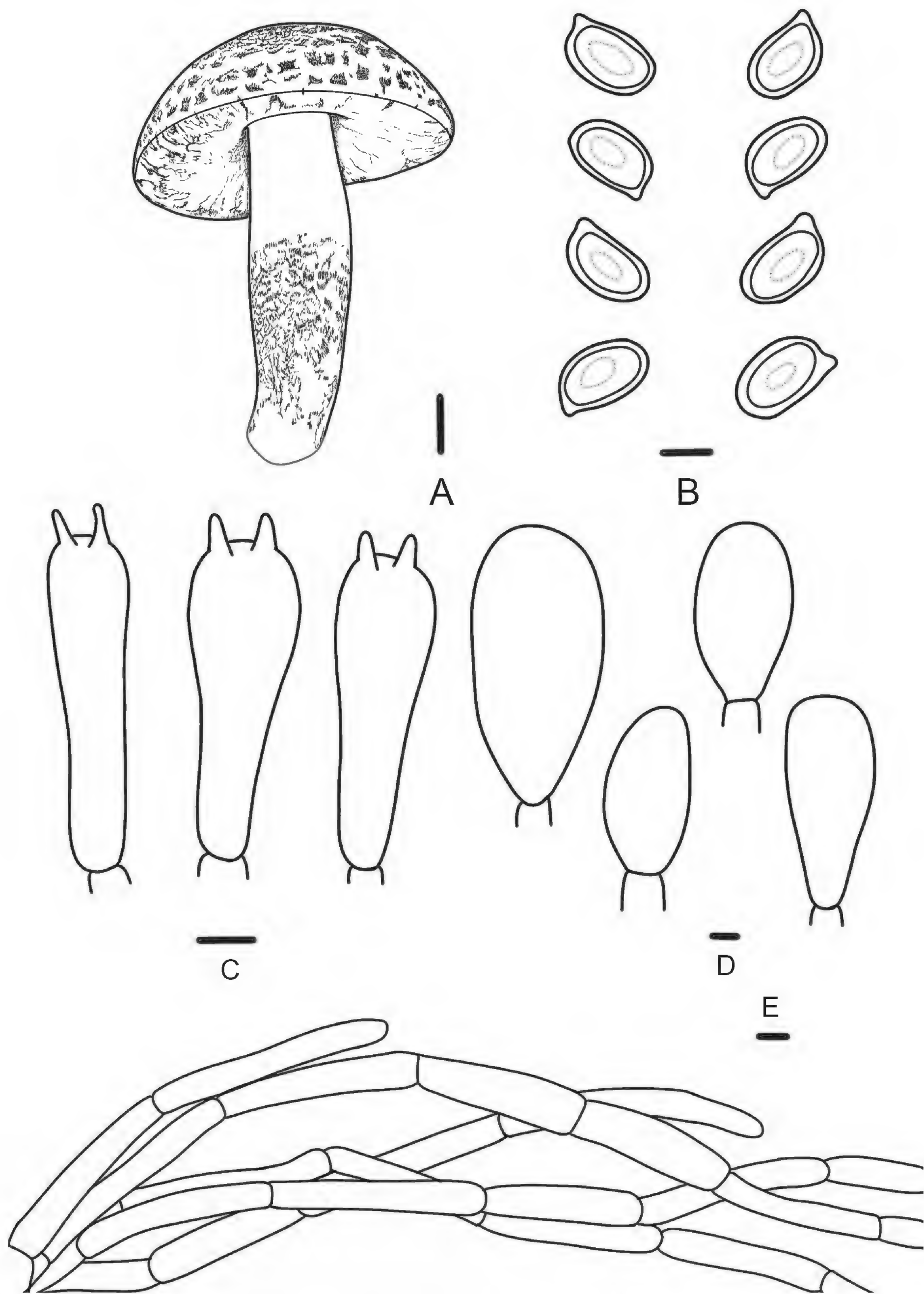


Figure 5. *Agaricus shenzhenensis* (FFAAS 3397, FFAAS 3398); **A.** Basidiomata; **B.** Basidiospores; **C.** Basidia; **D.** Cheilocystidia; **E.** Pileipellis. Scale bar: 1 cm (**A**); 5 μ m (**B–E**).

Notes. *Agaricus shenzhenensis* belongs to *A.* (subg. *Pseudochitonina*) sect. *Catenulati*, which currently comprises three species: *A. arabiensis* S. Hussain & Al-Sadi, *A. lannaensis* N. Suwannarach, J. Kumla & S. Lumyong and *A. malakandensis*.

Agaricus shenzhenensis differs from all three in both morphological and molecular characters. *Agaricus arabiensis* exhibits a reddish-brown to dark reddish-brown pileus, context unchanged on handling, smooth stipe, and globose to subglobose or broadly clavate, regularly catenulate cheilocystidia (Hussain et al. 2022). *Agaricus lannaensis* differs in having brown pileus, reddish brown context when cut, fibrillose stipe white below the annulus to the base, and smaller basidia (19–26 × 5.5–8.5 µm) (Jaichaliaw et al. 2021). *Agaricus malakandensis* possesses a dark brown to reddish brown pileus, smooth or fibrillose to slightly squamulose stipe, and multiseptate cheilocystidia with clavate to pyriform terminal element (Nawaz et al. 2024). Notably, catenulate cheilocystidia were not observed in this species, even though this feature is the primary morphological diagnostic characteristic for taxa within this section.

The genetic distinctions between *A. shenzhenensis* and *A. malakandensis* remain unequivocal, with four nucleotide differences in the ITS region, one in nrLSU, and four in *tef1-α* (Table 2). To ensure the accuracy of the results, we rechecked the quality of the sequences and confirmed their compliance with the required standards.

Notably, this species represents the first record of *A.* sect. *Catenulati* in China, expanding the known biogeographic range of this section.

Table 2. Variable loci of *A. malakandensis* and *A. shenzhenensis*. Position numbering based on ITS/nrLSU/*tef1-α* alignment. “–” means no relevant genetic information.

| Sample | ITS | | | | nrLSU | <i>tef1-α</i> | | | |
|-------------------------|-----|-----|-----|-----|-------|---------------|-----|-----|-----|
| | 256 | 273 | 286 | 646 | 410 | 288 | 399 | 439 | 503 |
| <i>A. malakandensis</i> | | | | | | | | | |
| ViL-60 T | C | T | C | C | C | G | A | C | C |
| ViL-68 | C | T | C | C | C | – | – | – | – |
| LD2012162 | C | T | C | C | C | G | A | C | C |
| <i>A. shenzhenensis</i> | | | | | | | | | |
| FFAAS 3397 T | T | C | T | T | G | A | T | T | T |
| FFAAS 3398 | T | C | T | T | G | A | T | T | T |

Discussion

Of the 26 recently described *Agaricus* species, five, *A. calolepidotus*, *A. xalapensis*, *A. karakensis*, *A. palodensis* and *A. wayanadensis*, were delineated solely through ITS sequence data (Arya and Pradeep 2024; Guzmán-Guillermo et al. 2024; Ullah et al. 2024), without multi-locus phylogenetic analyses. The same applies to *A. totalaiensis*, which is currently under review. Notably, the original description of *A. karakensis* lacks explicit GenBank accession numbers for its molecular data (Ullah et al. 2024). However, phylogenetic analyses of *Agaricus* based exclusively on ITS sequences lack methodological rigor (Cao et al. 2020). To ensure taxonomic reliability, the description of novel *Agaricus* species should integrate analyses of multi-locus (e.g., ITS + nrLSU + *tef1-α*). Furthermore, resolving higher-level phylogenetic relationships using single-copy orthologous genes derived from genomic data (He et al. 2024; Wang et al. 2024) is emerging as a trend.

Convergent evolution is a notable phenomenon within *Agaricus*, exemplified by striking macro-morphological similarities between *A. aurantifibrillosus* and *A. aurantipileatus*. Remarkably, this convergence extends beyond intra-generic boundaries, as seen in *A. sinoagrocyboides* T. Bau & S.E. Wang, a species our team previously discovered in China, which exhibits macroscopic traits strongly resembling those of *Agrocybe* species (Wang and Bau 2024). Such morphological variability becomes more complex in certain identifications due to the ecological plasticity of *Agaricus*. For instance, the fact that *A. subiculosus* is growing on decaying wood challenges traditional habitat assumptions for *Agaricus* (Parra et al. 2024a). These observations underscore the necessity of collecting morphologically ambiguous specimens during field surveys, as overlooked specimens may represent cryptic lineages or novel ecological adaptations within *Agaricus*.

During our field surveys targeting *Agaricus* specimens, we inadvertently collected specimens of the genera *Leucoagaricus*, *Leucocoprinus*, *Micropsalliota* and *Xanthagaricus*. These specimens will undergo comprehensive morphological and molecular analyses to explore potential novel discoveries.

Acknowledgements

The first author gratefully acknowledges Prof. Tolgor Bau (Jilin Agricultural University) for his foundational mentorship in taxonomic methodology during the first author's graduate studies. The first author is also deeply grateful to Cheng-Cheng for providing critical fungal specimens. We are grateful to Bin-Rong Ke from the Fungarium of the Fujian Academy of Agricultural Sciences for his assistance with specimen deposit. Special thanks are extended to DeepSeek (<https://www.deepseek.com>) for their professional assistance in translation. Finally, the authors extend our gratitude to the anonymous reviewers and the responsible editor, whose corrections and suggestions have made the publication of this work possible.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Funding

This research was financed by the National Key R&D Program of China (Project Nos. 2023YFD1600501) and the China-Aid Agro-Tech Coop. Project in FSM PhaseXII.

Author contributions

SEW: Conceptualization, Investigation, Methodology, Resources, Software, Validation, Writing original draft preparation, Writing review and editing. PHL, DML: Conceptualization, Resources, Validation, Writing review and editing. SAC: Conceptualization, Investigation, Resources. HCH: Resources, Validation.

Author ORCIDs

Shi-en Wang  <https://orcid.org/0009-0002-0710-0728>

Si-ang Chen  <https://orcid.org/0009-0007-7315-8107>

Data availability

All of the data that support the findings of this study are available in the main text, or in publicly accessible data repositories, as indicated in the text.

References

- Arya CP, Pradeep CK (2024) *Agaricus* section *Minores*: New and noteworthy species from India. *Phytotaxa* 634: 255–273. <https://doi.org/10.11646/phytotaxa.634.3.5>
- Bashir H, Asif M, Ghafoor A, Niazi AR, Khalid AN, Parveen G, Harun N, Afshan N-S, Bibi A, Callac P (2024) Multigene phylogeny and morphological descriptions of five species of *Agaricus* sect. *Minores* from subtropical climate zones of Pakistan. *PLOS ONE* 19: e0302222. <https://doi.org/10.1371/journal.pone.0302222>
- Bau T (2018) *Mushroom Taxonomy*. Science Press, Beijing, China, 303 pp.
- Boxshall AG, Birch JL, Lebel T, Symonds MRE, Callahan DL (2021) A field-based investigation of simple phenol variation in Australian *Agaricus xanthodermus*. *Mycologia* 113: 1123–1135. <https://doi.org/10.1080/00275514.2021.1936851>
- Callac P, Chen J (2018) Tropical species of *Agaricus*. In: Sánchez JE, Mata G, Royse DJ (Eds) *Tropical Mushrooms*. El Colegio de la Frontera Sur, Chiapas, Mexico, 25–38.
- Cao B, He MQ, Ling ZL, Zhang MZ, Wei SL, Zhao RL (2020) A revision of *Agaricus* section *Arvenses* with nine new species from China. *Mycologia* 113: 191–211. <https://doi.org/10.1080/00275514.2020.1830247>
- Chen J, Callac P, Parra LA, Karunarathna SC, He MQ, Moinard M, De Kesel A, Raspé O, Wisitrassameewong K, Hyde KD, Zhao RL (2017) Study in *Agaricus* subgenus *Minores* and allied clades reveals a new American subgenus and contrasting phylogenetic patterns in Europe and Greater Mekong Subregion. *Persoonia* 38: 170–196. <https://doi.org/10.3767/003158517X695521>
- Crous PW, Wingfield MJ, Jurjević Ž, Balashov S, Osieck ER, Marin-Felix Y, Luangsa-ard JJ, Mejía LC, Cappelli A, Parra LA, Lucchini G, Chen J, Moreno G, Faraoni M, Zhao RL, Weholt Ø, Borovička J, Jansen GM, Shivas RG, Tan YP, Akulov A, Alfenas AC, Alfenas RF, Altés A, Avchar R, Barreto RW, Catcheside DEA, Chi TY, Esteve-Raventós F, Fryar SC, Hanh LTM, Larsbrink J, Oberlies NH, Olsson L, Pancorbo F, Raja HA, Thanh VN, Thuy NT, Ajithkumar K, Akram W, Alvarado P, Angeletti B, Arumugam E, Khalilabad AA, Bandini D, Baroni TJ, Barreto GG, Boertmann D, Bose T, Castañeda Ruiz RF, Couceiro A, Cykowska-Marzencka B, Dai YC, Darmostuk V, da Silva SBG, Dearnaley JDW, de Azevedo Santiago ALCM, Declercq B, de Freitas LWS, De la Peña-Lastra S, Delgado G, de Lima CLF, Dhotre D, Dirks AC, Eisvand P, Erhard A, Ferro LO, García D, García-Martín A, Garrido-Benavent I, Gené J, Ghobad-Nejhad M, Gore G, Gunaseelan S, Gusmão LFP, Hammerbacher A, Hernández-Perez AT, Hernández-Restrepo M, Hofmann TA, Hubka V, Jiya N, Kaliyaperumal M, Keerthana KS, Ketabchi M, Kezo K, Knoppersen R, Kolarczykova D, Kumar TKA, Læssøe T, Langer E, Larsson E, Lodge DJ, Lynch MJ, Maciá-Vicente JG, Mahadevakumar S, Mateos A, Mehrabi-Koushki M, Miglio BV, Noor A, Oliveira JA, Pereira OL, Piątek M, Pinto A, Ramírez GH, Raphael B, Rawat G, Renuka M, Reschke K, Mateo AR, Saar I, Saba M, Safi A, Sánchez RM, Sandoval-Denis M, Savitha AS, Sharma A, Shelke D, Sonawane H, Souza MGAP, Stryjak-Bogacka M, Thines M, Thomas A, Torres-Garcia D, Traba JM, Vauras J, Vermaas M, Villarreal M, Vu D, Whiteside EJ, Zafari D, Starink-Willemse M, Groenewald JZ (2024) Fungal Planet description sheets: 1697–1780. *Fungal Systematics and Evolution* 14: 325–577. <https://doi.org/10.3114/fuse.2024.14.19>

- Donk MA (1962) The generic names proposed for Agaricaceae. Schweizerbart Science Publishers, Stuttgart, Germany, 320 pp.
- Gardes M, Bruns TD (1993) ITS primers with enhanced specificity for basidiomycetes—application to the identification of mycorrhizae and rusts. *Molecular Ecology* 2: 113–118. <https://doi.org/10.1111/j.1365-294X.1993.tb00005.x>
- Guindon S, Dufayard JF, Lefort V, Anisimova M, Hordijk W, Gascuel O (2010) New algorithms and methods to estimate maximum-likelihood phylogenies: Assessing the performance of PhyML 3.0. *Systematic Biology* 59: 307–321. <https://doi.org/10.1093/sysbio/syq010>
- Guzmán-Guillermo J, Chen J, Enríquez-Bedolla JC, Oros-Ortega I, Zetina-Córdoba P, Núñez-Pastrana R, Llarena-Hernández RC (2024) Morphological characteristics and phylogenetic analyses revealed two new species of *Agaricus* subg. *Minoriopsis* from Mexico. *Phytotaxa* 655: 65–78. <https://doi.org/10.11646/phytotaxa.655.1.5>
- Hall TA (1999) BioEdit: A User-Friendly Biological Sequence Alignment Editor and Analysis Program for Windows 95/98/NT. *Nucleic Acids Symposium Series* 41: 95–98. <https://doi.org/10.1021/bk-1999-0734.ch008>
- He MQ, Chuankid B, Hyde KD, Cheewangkoon R, Zhao RL (2018a) A new section and species of *Agaricus* subgenus *Pseudochitonina* from Thailand. *Mycosphaera* 40: 53–67. <https://doi.org/10.3897/mycokeys.40.26918>
- He MQ, Hyde KD, Si W, Yi X, Zhao RL (2018b) Three new species of *Agaricus* section *Minores* from China. *Mycosphere: Journal of Fungal Biology* 9: 189–201. <https://doi.org/10.5943/mycosphere/9/2/3>
- He MQ, Wang MQ, Chen ZH, Deng WQ, Li TH, Vizzini A, Jeewon R, Hyde KD, Zhao RL (2022) Potential benefits and harms: A review of poisonous mushrooms in the world. *Fungal Biology Reviews* 42: 56–68. <https://doi.org/10.1016/j.fbr.2022.06.002>
- He MQ, Cao B, Liu F, Boekhout T, Denchev TT, Schoutteten N, Denchev CM, Kemler M, Gorjón SP, Begerow D, Valenzuela R, Davoodian N, Niskanen T, Vizzini A, Redhead SA, Ramírez-Cruz V, Papp V, Dudka VA, Dutta AK, García-Sandoval R, Liu XZ, Kijpornyongpan T, Savchenko A, Tedersoo L, Theelen B, Trierveiler-Pereira L, Wu F, Zamora JC, Zeng XY, Zhou LW, Liu SL, Ghobad-Nejhad M, Giachini AJ, Li GJ, Kakishima M, Olariaga I, Haelewaters D, Sulistyo B, Sugiyama J, Svantesson S, Yurkov A, Alvarado P, Antonín V, da Silva AF, Druzhinina I, Gibertoni TB, Guzmán-Dávalos L, Justo A, Karunarathna SC, Galappaththi MCA, Toome-Heller M, Hosoya T, Liimatainen K, Márquez R, Mešić A, Moncalvo JM, Nagy LG, Varga T, Orihara T, Raymundo T, Salcedo I, Silva-Filho AGS, Tkalčec Z, Wartchow F, Zhao C-L, Bau T, Cabarro-Hernández M, Cortés-Pérez A, Decock C, De Lange RB, Weiss M, Menolli N, Nilsson RH, Fan Y-G, Verbeken A, Gafforov Y, Meiras-Ottoni A, Mendes-Alvarenga RL, Zeng N-K, Wu Q, Hyde KD, Kirk PM, Zhao R-L (2024) Phylogenomics, divergence times and notes of orders in basidiomycota. *Fungal Diversity* 126: 127–406. <https://doi.org/10.1007/s13225-024-00535-w>
- Hussain S, Al-Kharousi M, Al-Muharabi MA, Al-Maqbali D, Al-Shabibi Z, Al-Balushi AH, Al-Yahya’ei MN, Saady NA, Abdel-Jalil R, Velazhahan R, Al-Sadi AM (2022) Phylogeny of *Agaricus* subgenus *Pseudochitonina* with the description of a new section and a new species from Oman. *Mycological Progress* 21(72): 1–13. <https://doi.org/10.1007/s11557-022-01819-8>
- Jaichaliaw C, Kumla J, Vadthanarat S, Suwannarach N, Lumyong S (2021) Multigene phylogeny and morphology reveal three novel species and a novel record of *Agaricus* from Northern Thailand. *Frontiers in Microbiology* 12(650513): 1–14. <https://doi.org/10.3389/fmicb.2021.650513>

- Kalyaanamoorthy S, Minh BQ, Wong TKF, von Haeseler A, Jermiin LS (2017) ModelFinder: Fast model selection for accurate phylogenetic estimates. *Nature Methods* 14: 587–589. <https://doi.org/10.1038/nmeth.4285>
- Katoh K, Standley DM (2013) MAFFT multiple sequence alignment software version 7: Improvements in performance and usability. *Molecular Biology and Evolution* 30: 772–780. <https://doi.org/10.1093/molbev/mst010>
- Kerrigan RW (2016) *Agaricus* of North America. New York Botanic Garden Press, New York, USA, 573 pp.
- Kornerup A, Wanscher JHK (1978) The Methuen Handbook of Colour. 3rd edition. Methuen Publishing Ltd, London, UK, 256 pp.
- Lebel T (2013) Two new species of sequestrate *Agaricus* (section *Minores*) from Australia. *Mycological Progress* 12: 699–707. <https://doi.org/10.1007/s11557-012-0879-x>
- Liang YS, Huang XX, Lin ZJ, He DL, Qiu LH (2024) Three new species of *Agaricus* from Baiyun Mountain, Guangzhou, China. *Mycologia* 116: 431–448. <https://doi.org/10.1080/00275514.2024.2311039>
- Liu AQ, Dai RC, Zhang MZ, Cao B, Xi YL, Wei SL, Zhao RL (2020) Species of *Agaricus* section *Agaricus* from China. *Phytotaxa* 452: 1–18. <https://doi.org/10.11646/phytotaxa.452.1.1>
- Liu SL, Wang XW, Li GJ, Deng CY, Rossi W, Leonardi M, Liimatainen K, Kekki T, Niskanen T, Smith ME, Ammirati J, Bojantchev D, Abdel-Wahab MA, Zhang M, Tian EJ, Lu YZ, Zhang JY, Ma J, Dutta AK, Acharya K, Du TY, Xu JZ, Kim JS, Lim YW, Gerlach A, Zeng NK, Han YX, Razaghi P, Raza M, Cai L, Calabon MS, Jones EBG, Saha R, Kumar TKA, Krishnapriya K, Thomas A, Kaliyaperumal M, Kezo K, Gunaseelan S, Singh SK, Singh PN, Lagashetti AC, Pawar KS, Jiang SH, Zhang C, Zhang H, Qing Y, Bau T, Peng XC, Wen TC, Ramirez NA, Niveiro N, Li MX, Yang ZL, Wu G, Tarafder E, Tennakoon DS, Kuo CH, da Silva TM, Souza-Motta CM, Bezerra JDP, He G, Ji XH, Suwannarach N, Kumla J, Lumyong S, Wannathes N, Rana SWL, Hyde KD, Zhou LW (2024) Fungal diversity notes 1717–1817: Taxonomic and phylogenetic contributions on genera and species of fungal taxa. *Fungal Diversity* 124: 1–216. <https://doi.org/10.1007/s13225-023-00529-0>
- Moncalvo JM, Lutzoni FM, Rehner SA, Johnson J, Vilgalys R (2000) Phylogenetic relationships of agaric fungi based on nuclear large subunit ribosomal DNA sequences. *Systematic Biology* 49: 278–305. <https://doi.org/10.1093/sysbio/49.2.278>
- Mou GF, Bau T (2021) *Asproinocybaceae* fam. nov. (Agaricales, Agaricomycetes) for accommodating the genera *Asproinocybe* and *Tricholosporum*, and description of *Asproinocybe sinensis* and *Tricholosporum guangxiense* sp. nov. *Journal of Fungi* (Basel, Switzerland) 7(1086): 1–22. <https://doi.org/10.3390/jof7121086>
- Nawaz R, Murad W, Irshad M, Callac P, Hussain S (2024) *Agaricus* subgenus *Pseudochiton* in Malakand, Pakistan: An updated phylogeny and description of three new species. *Mycologia* 116: 577–600. <https://doi.org/10.1080/00275514.2024.2334473>
- Nguyen LT, Schmidt HA, von Haeseler A, Minh BQ (2015) IQ-TREE: A fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Molecular Biology and Evolution* 32: 268–274. <https://doi.org/10.1093/molbev/msu300>
- Ortiz-Santana B, Chen J, Parra LA, Angelini C, Lodge DJ, Kerrigan RW, Callac P (2021) The genus *Agaricus* in the Caribbean II. Refined phylogeny of *Agaricus* subg. *Spissicaules* with description of two new sections and eight new species. *Mycological Progress* 20: 381–411. <https://doi.org/10.1007/s11557-021-01686-9>
- Palestina-Villa EN, Garibay-Orijel R, Chen J, Parra LA, Águila B, Medel-Ortiz R (2024) *Agaricus cervinoculus* sp. nov. (Agaricaceae), a new wild edible mushroom from Mexico. *Phytotaxa* 642: 229–241. <https://doi.org/10.11646/phytotaxa.642.4.1>

- Parra LA (2008) *Agaricus* L. *Allopsalliota* Nauta & Bas, Part 1; Fungi Europaei 1. Edizioni Candusso, Alassio, Italy, 823 pp.
- Parra LA (2013) *Agaricus* L. *Allopsalliota* Nauta & Bas, Part 2; Fungi Europaei. Edizioni Candusso, Alassio, Italy, 1168 pp.
- Parra LA, Angelini C, Ortiz-Santana B, Mata G, Billette C, Rojo C, Chen J, Callac P (2018a) The genus *Agaricus* in the Caribbean. Nine new taxa mostly based on collections from the Dominican Republic. *Phytotaxa* 345: 219–271. <https://doi.org/10.11646/phytotaxa.345.3.2>
- Parra LA, Cappelli A, Kerrigan RW, Bizio E (2018b) *Agaricus porphyrocephalus* subsp. *alpinus* a new subspecies collected in the Italian Alps. *Micologia e Vegetazione Mediterranea* 33(2): 67–88.
- Parra LA, Angelini C, Miller KO, Chen J (2024a) *Agaricus subiculosus*, a new species of the genus *Agaricus* sect. *Minores* from Puerto Rico (USA). *MycolObs - Mycological Observations* 8: 33–43.
- Parra LA, Cappelli A, Bizio E, Ferrari RJ, Weholt Ø, Fellin A, Chen J (2024b) *Agaricus manzollii* and *Agaricus permianus* two new species in *Agaricus* sect. *Minores*. *Rivista Micologica Romana, Bolletino dell'Associazione Micologica Ecologica Romana* 122(2): 32–46. <https://doi.org/10.57624/AMER.2024.5>
- Rehner SA, Buckley E (2005) A *Beauveria* phylogeny inferred from nuclear ITS and EF1- α sequences: Evidence for cryptic diversification and links to *Cordyceps* teleomorphs. *Mycologia* 97: 84–98. <https://doi.org/10.3852/mycologia.97.1.84>
- Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MrBayes 3.2: Efficient bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61: 539–542. <https://doi.org/10.1093/sysbio/sys029>
- Ullah T, Ullah K, Kamal A, Saba M (2024) *Agaricus karakensis* sp. nov. (Agaricaceae, Agaricales), a new species from Pakistan. *Phytotaxa* 658: 191–202. <https://doi.org/10.11646/phytotaxa.658.2.6>
- Wang SE (2024) Studies on the Species Resources and Domestication Culture of *Agaricus* from Northeast China. Master's thesis. Jilin Agricultural University, Changchun, China.
- Wang SE, Bau T (2024) Six New Species of *Agaricus* (Agaricaceae, Agaricales) from Northeast China. *Journal of Fungi* (Basel, Switzerland) 10: 59. <https://doi.org/10.3390/jof10010059>
- Wang GS, Cai Q, Hao YJ, Bau T, Chen ZH, Li MX, David N, Kraisitudomsook N, Yang ZL (2024) Phylogenetic and taxonomic updates of Agaricales, with an emphasis on *Tricholomopsis*. *Mycology* 15: 180–209. <https://doi.org/10.1080/21501203.2023.2263031>
- White TJ, Bruns T, Lee S, Taylor J (1990) Amplification and Direct Sequencing of Fungal Ribosomal RNA Genes for Phylogenetics. In: Innis MA, Gelfand DH, Sninsky JJ, White TJ (Eds) *PCR Protocols, a Guide to Methods and Applications*, 315–322. <https://doi.org/10.1016/B978-0-12-372180-8.50042-1>
- Wisitrassameewong K, Karunarathna SC, Thongklang N, Zhao RL, Callac P, Moukha S, Férandon C, Chukeatirote E, Hyde KD (2012) *Agaricus subrufescens*: A review. *Saudi Journal of Biological Sciences* 19: 131–146. <https://doi.org/10.1016/j.sjbs.2012.01.003>
- Wu F, Zhou LW, Yang ZL, Bau T, Li TH, Dai YC (2019) Resource diversity of Chinese macrofungi: Edible, medicinal and poisonous species. *Fungal Diversity* 98: 1–76. <https://doi.org/10.1007/s13225-019-00432-7>

- Zhang D, Gao FL, Jakovlić I, Zou H, Zhang J, Li WX, Wang GT (2020) PhyloSuite: An integrated and scalable desktop platform for streamlined molecular sequence data management and evolutionary phylogenetics studies. *Molecular Ecology Resources* 20: 348–355. <https://doi.org/10.1111/1755-0998.13096>
- Zhao RL, Karunarathna S, Raspé O, Parra LA, Guinberteau J, Moinard M, De Kesel A, Barroso G, Courtecuisse R, Hyde KD, Guelly AK, Desjardin DE, Callac P (2011) Major clades in tropical *Agaricus*. *Fungal Diversity* 51: 279–296. <https://doi.org/10.1007/s13225-011-0136-7>
- Zhao RL, Hyde KD, Karunarathna SC, Hyde KD, Desjardin DE, Raspé O, Soyong K, Guinberteau J, Callac P (2012) *Agaricus flocculosipes* sp. nov., a new potentially cultivatable species from the palaeotropics. *Mycoscience* 53: 300–311. <https://doi.org/10.1007/S10267-011-0169-5>
- Zhao RL, Zhou JL, Chen J, Margaritescu S, Sánchez-Ramírez S, Hyde KD, Callac P, Parra LA, Li GJ, Moncalvo JM (2016) Towards standardizing taxonomic ranks using divergence times – a case study for reconstruction of the *Agaricus* taxonomic system. *Fungal Diversity* 78: 239–292. <https://doi.org/10.1007/s13225-016-0357-x>
- Zhou JL, Su SY, Su HY, Wang B, Callac P, Guinberteau J, Hyde KD, Zhao RL (2016) A description of eleven new species of *Agaricus* sections *Xanthodermatei* and *Hondenses* collected from Tibet and the surrounding areas. *Phytotaxa* 257: 99–121. <https://doi.org/10.11646/phytotaxa.257.2.1>